MONITORING GROWTH AND DIET OF NESTLING RHINOCEROS AUKLETS TO GAUGE PREY AVAILABILITY

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ABSTRACT

As part of an investigation to develop a long term monitoring program of seabird populations in British Columbia we assesed nestling growth and diet as a potential indicator of fish prey populations. From 1984 to 1986 we studied growth and diet of nestling Rhinoceros Auklets (Cerorhinca monocerata) on three colonies off the B.C. coast: Lucy, Pine and Triangle islands. In all years chicks on Lucy Is. were fed most and grew fastest while birds on Pine I. were fed least (except in 1985) and grew slowest. Nestlings on Triangle I. were intermediate between Lucy and Pine islands. Not only was the ranking of the colonies the same within years but chick growth rates on all three colonies varied in unison between years. We suggest that variation in the growth rate of nestlings within and between years is related to the availability of Pacific sandlance (Ammodytes hexapterus), a principal prey species of Rhinoceros Auklets in B.C. during July. We conclude that data on chick growth and diet collected on a number of well separated colonies may indicate sandlance availability, and provide a useful index of ocean feeding conditions. We suggest that the Rhinoceros Auklet is an appropriate species with which to develop a long-term monitoring program for coastal seabirds in B.C. and discuss the importance of implementing such a program on Canadas' west coast.

Résumé

Lors d'une étude visant à développer une méthode de suivi à long terme des populations d'alcidés de Colombie Britannique, nous avons évalué la possibilité d'utiliser les courbes de croissance de jeunes et leur diète comme indicateur de l'état des populations de poissons. De 1984 à 1986 nous avons étudié la croissance et la diète de jeunes Alques Cornus (Cerorhinca monocerata) dans trois colonies de Colombie Britannique: soit les îles Lucy, Pine et Triangle.

Au cours des trois années d'études, les jeunes Alques Cornus de l'île Lucy reçurent plus de nourriture et se développèrent plus rapidement que ceux des îles Pine et Triangle. Les jeunes de l'île Pine reçurent moins de nourriture (à l'exception de 1985) et se développèrent plus lentement que ceux de l'île Triangle. Les conditions sur l'île Triangle etaient intermediaires entre celles sur les îles Lucy et Pine. L'ordre des colonies fut le même chaque année et la croissance des jeunes varia à l'unisson parmi les colonies au cours des trois années. Nous suggerons que la variation dans la croissance des jeunes à l'intérieur et entre les années est reliée à la disponibilité du lancon du Pacifique (Ammodytes hexapterus), une des proies principales de l'Alque Cornu en Colombie Britannique en juillet. Nous concluons que les données sur la croissance des jeunes et leur diète, prises dans plusieurs colonies distantes, peuvent indiquer la disponibilité du lancon du Pacifique et réfléter les conditions d'alimentations en Mer. Nous suggerons que l'Alque Cornu est une espece appropriee pour developer un systeme de suivi à long terme pour les alcidés côtiers de Colombie Britannique. Finalement nous discutons l'importance d'implémenter un tel programme la côte ouest du Canada.

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TABLE OF CONTENTS

Publication data ii

Abstract iii

Résumé iv

Acknowledgements v

1. INTRODUCTION 1

2. METHODS 3

2.1 Study species 3

2.2 Study sites 4

2.3 Study methods 6

3. RESULTS 11

3.1 Chick age at first weighing 11

3.2 Chick growth 11

3.3 Nestling diet 14

3.3.1 Weight of bill loads 14

3.3.2 Composition of bill loads 20

3.3.3 Year-classes of sandlance in bill loads 20

3.3.4 Caloric values of bill loads 24

4. DISCUSSION 26

5. MANAGEMENT RECOMMENDATIONS 34

6. LITERATURE CITED 39

APPENDIX 1: The pilot study on Lucy Islands in 1983 43

APPENDIX 2. Equations of composite growth curves 44

APPENDIX 3: Additional prey species of Rhinoceros Auklets ... 45

1. INTRODUCTION

Monitoring the diet and/or growth of nestling seabirds may be a cheap and convenient means of monitoring changes in prey fish populations (Ashmole and Ashmole, 1968; Ricklefs and White, 1975; Vermeer and Cullen, 1979; Wehle, 1983; Ricklefs et al., 1984; Vermeer and Westrheim, 1984; Furness and Barrett, 1985; Barrett et al., 1987; Nariko et al.,1987). Hislop and Harris (1983) independently measured fish abundance and the diet of nestling Atlantic Puffins (Fratercula arctica), and found a close correspondence between the two.

In British Columbia (B.C.), there is increased demand for and stress exerted on the natural resources of the coast. Part of Canadian Wildlife Service's responsibility as a conservation agency is to detect the impact of man-made changes on Migratory Birds which include the colonial seabirds. At present, population surveys and monitoring of seabirds largely depends on counting the number of burrows in colonies and measuring their occupancy rate. This is an expensive and time consuming procedure that offers only indirect evidence of problems and may detect impacts years after the causes have disappeared . The study of nestling growth and diet is part of an attempt to develop a monitoring program that should allow us to identify and understand the current stresses on populations and the responses of the birds to them.

The objective of this study is to show how growth and diet of nestling Rhinoceros Auklets may reflect changes in availability of fish prey in surface waters. Similar patterns in chick diet and growth on widely separated colonies would suggest that fluctuations in prey availability occur over broad geographic areas and are not strictly local phenomena. Information on the status of prey fish populations is a key factor in the development and establishment of a long-term monitoring program for coastal seabirds in B.C.

Rhinoceros Auklets were chosen as our study species because they occur at widely separated localities on the B.C. coast and because they can be easily monitored with little disturbance to nesting birds. In addition, other studies of Rhinoceros Auklets in Washington state (Richardson, 1961; Leschner, 1976; Wilson, 1977; Wilson and Manuwal, 1986), British Columbia (Vermeer, 1979,1980; Vermeer and Cullen, 1979; Vermeer and Westrheim, 1984; Bertram, 1988), and Alaska (Hatch, 1984) provide us with extensive comparative data.

2. METHODS

2.1 Study species

Rhinoceros Auklets are confined to the Pacific Ocean with colonies in Japan, U.S.S.R., Alaska, British Columbia, Washington, Oregon and California (Vermeer, 1979). The Rhinoceros Auklet is colonial and piscivorous, and lays a single egg clutch in a burrow. In Washington stat,e egg laying occurs between 30 April to 7 May (Wilson and Manuwal, 1986). Eggs are incubated from 39 to 52 days with an average of 45 days and following hatching, the downy chicks are brooded, on average, for four days (Wilson and Manuwal, 1986). Rhinoceros Auklets "fly" underwater to catch fish which they feed their chicks. A parent may deliver one very large fish (up to 80 g, Vermeer and Devito, 1986) or up to 21 smaller fish carried cross-wise in its bill. In B.C., Pacific sandlance is the dominant prey on most colonies in July. On inshore islands, Pacific herring (Clupea harengus) is also important while Pacific saury (Cololabis saira) and rockfish (Sebastes spp.) tend to be important on offshore islands. A number of other fish are taken less frequently. (see Vermeer and Westrheim, 1984). Prey taken may vary within and between seasons, and between colonies (Vermeer, 1980; Vermeer and Westrheim, 1984). Parents return to the colony at night to provision their chicks and depart before sunrise (see Wilson and Manuwal, 1986). Parents generally make one trip each to the burrow every night, although Richardson (1961)

reports instances of three visits to a single burrow in one night. Some nights, however, neither parent visits and chicks receive nothing (Bertram, 1988). Rhinoceros Auklet growth is among the slowest in the Alcidae. Chicks fledge between 51 and 80 percent (250-400 g) of adult weight (Vermeer and Cullen, 1979; Bertram,1988) between 45 and 60 days of age. The young complete their development at sea following fledging. Band returns suggest that Rhinoceros Auklets from British Columbia winter in the waters off California and Oregon (Kaiser et al., 1984).

2.2 Study sites

We studied Rhinoceros Auklets on three of the largest colonies in B.C.- Lucy, Pine, and Triangle islands. Estimates of the size of the breeding populations are provided by Kaiser and Lemon (1987). The location of these colonies is shown in Figure 1.

Lucy Islands (54° 18' N; 130° 37' W) are an archipelago of small, low lying, heavily forested islands containing approximately 21,500 breeding pairs. They are located in Chatham Sound 18 kilometres west of Prince Rupert.

Pine Island (50° 58' N; 127° 41' W) is heavily forested and low lying with an estimated 67,000 breeding pairs. It is 10 km off the N.E. end of Vancouver Island and is immediately adjacent to the Storm Islands with an additional estimated 73,000 pairs.

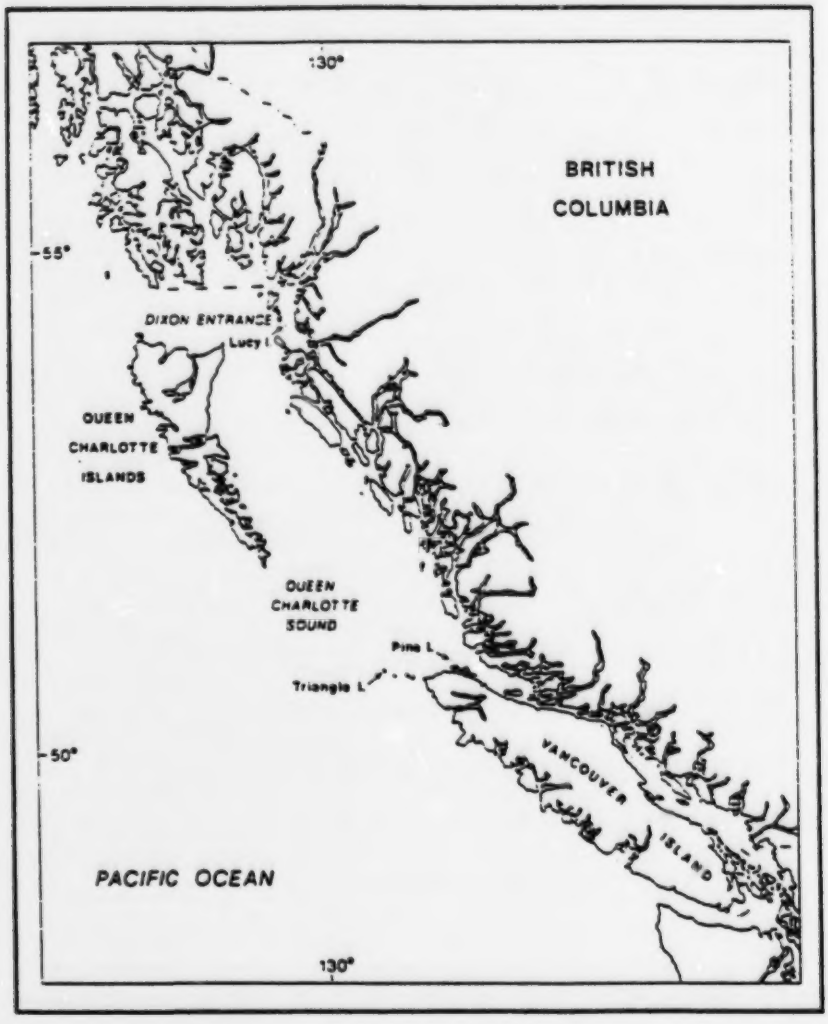

Figure 1: The locations of Lucy, Pine and Triangle islands on the coast of British Colombia (from Vermeer and Westrheim, 1984).

Triangle Island (50° 52' N; 129° 05' W), outermost of the Scott Island Group, is an exposed, treeless, steep-sloped island 40 km off the northwest tip of Vancouver Island. It is B.C.'s largest seabird colony and contains about 22,000 breeding pairs of Rhinoceros Auklets (Butler et al., 1985) among half a million pairs of other seabirds. The climate, flora and fauna have been described by Carl et al. (1951) and Vermeer et al. (1976).

2.3 Study methods

In July of 1984, 1985, and 1986 field crews visited each colony to conduct synchronous studies of chick growth and diet. Lucy was also the site of a pilot study in 1983 (Appendix 1). Upon arrival at a colony, a sample of chicks was obtained by excavating their burrows. On Triangle soil is relatively scarce, and burrows are short, averaging about 1 m long. They are often found underneath tussocks of grass, wedged beteen walls of rock. Burrows on Lucy (one up to 5 m) and Pine are longer and many have branching tunnels and multiple entrances. The tunnels range from 1 cm to over 1 m deep (on Lucy), and frequently go under roots or open into underground caverns at the base of trees. Burrows were excavated with a trowel and pruning clippers to cut through small roots. When necessary, consecutive holes were dug along each burrow until the nest chamber was reached. The access holes were always recovered with sticks or cedar shingles and dirt to seal out light and to protect them from investigation by Ravens (Corvus corax) and other avian predators. Occupied

burrows were assigned a number and marked with flagging tape for relocation.

We constructed composite growth curves, as outlined by Ricklefs and White (1975), to make comparisons between colonies and years. This technique involves locating a sample of nestlings from a wide developmental range and measuring their wing lengths and weights on the same day. After a short period of development (we chose 10 days) the nestlings are remeasured. Using wing length to estimate age, a mass-age relationship or composite growth curve representing a hypothetical chick is constructed. According to Ricklefs and White (1975), composite growth curves may act as a biological indicator of marine ecological conditions at a particular time. To facilitate comparisons we chose to fit straight lines to the composite growth data from each year. We used a MANOVA procedure to compare slopes of growth curves and performed pairwise comparisons if differences between colonies within a year or differences between years on a single colony were detected.

As the study progressed we decided that the best technique for constructing composite curves involves locating a sample of occupied burrows and then measuring all the chicks in one or two days rather than piecemeal as they are discovered. This not only saves time during the second measurement but ensures that all chicks are growing over the same 10 day period, and thus experiencing similar conditions. Chicks were weighed to the nearest 2 g on an OHAUS Lume-o-gram electronic balance (model

D1001) at a recorded time. We also ringed nestlings with plastic bands to denote previous handling and fitted them with U.S. Fish and Wildlife Service stainles steel bands after reaching 200 g. Ten days later we tried to measure chicks at the same time to account for daily weight variation (Vermeer and Cullen, 1982). To age chicks we measured the flattened wing from the wrist to the fleshy tip, pin or feather tip, depending on the age of the chick. On all colonies, in all years the wing length growth curves were similar in shape. Therefore chick age was estimated using the wing length growth curve established from a sample of known age chicks in 1986 on Lucy Islands. Wing length is a reliable indicator of age since it varies little between fast and slow weight gaining birds within or between seasons (Asbirk, 1979; Vermeer and Cullen, 1979; Barrett et al., 1987).

The food of nestlings was sampled by capturing adults at night as they returned with fish for their young. Samples from individual adults were referred to as "bill loads" and were placed in separate plastic bags for measurement. Two or three sampling bouts were conducted during the course of the study at well spaced intervals. To minimize disturbance to the birds sampling in the colony never exceeded one and a half hours. Bill loads were never collected in areas where chick growth was being monitored. Bill loads were not collected on Triangle in 1985. Instead, the chicks' bills were taped closed to prevent feeding (c.f. Hatch, 1984). The uningested "burrow loads" were collected the following day, measured and then fed to the chicks. In 1986 on Lucy, bill loads were weighed but species composition was

determined from burrow loads collected using nylon hoods fitted to the chicks to prevent feeding (Bertram, 1988).

During the sampling of bill loads adults were occasionally weighed (to the nearest 2 g), banded with U.S. Fish and and Wildlife Service stainless steel bands, and then released. We used this information to compare adult weight between colonies. All samples from a single colony were combined as we had no way of differentiating the sexes or breeders from non-breeders.

Sandlance collected from bill loads were divided into two year-classes. Following the same procedure used by Vermeer and Westrheim (1984), we asssigned fish from 40 to 110 mm (snout to tail notch) to year-class-1 and those from 111 to 180 mm to year-class-2.

The caloric content of bill loads was calculated using Vermeer and Devito's (1986) results for caloric content (calories/gram dry weight) of common Rhinoceros Auklet prey. Our calculations however, were based on the wet weights of bill loads. As a result the average caloric content of bill loads from any colony is an overestimate of the actual average. Thus, comparisons between years and colonies are relative not absolute. No caloric value was available for kelp greenling (Hexagrammos decagrammus) so it was assigned the same caloric value as rockfish. Uncommon prey such as squid for which caloric content information was unavailable, were eliminated from calculations.

When replicate data was available from each colony in each year (eg. bill load data) we performed a two-way ANOVA (to look for interaction effects) followed by a series of one-way ANOVA's by year and by colony. One-way analyses were followed by a Student-Newman-Keuls multiple range test if significant differences were detected. The significance level throughout is 0.05.

3. RESULTS

3.1 Chick age at first weighing

In all years the first measurement of chicks used in the composite growth study took place in the first half of July. Within years there were no consistent differences between the ages of the chicks in different colonies. In 1984 chicks on Triangle were most advanced in age while the oldest chicks were found on Lucy in 1986 (Table 1).

Chicks tended to be oldest in 1985 and youngest in 1984, but the differences were only significant on Pine Island. Although the youngest chicks used were discovered on Lucy during the earliest excavations, the differences in chick age between years on Pine Island was probably real and was not a result of the timing of excavation since visits occurred during the same time frame in each year (Table 1).

3.2 Chick growth

In all years chicks on Lucy grew significantly faster than those on Pine and Triangle which had similar growth rates (Table 2). Growth rate ranged from 5.9 g/day on Pine in 1986 to 10.8 g/day on Lucy in 1985.

Between years in all colonies, chick growth rates tended to rise and fall in unison. In 1985, growth rates on all colonies

Table 1: Dates of first weighing and mean ages of chicks used to construct composite growth curves on Lucy (L), Pine (P), and Triangle (Tri.,T) islands in July 1984-86. Chick age was estimated from wing length. Statistics are given for interaction effects between colony and year, and for one-way ANOVA by colony and year, followed by paired comparisons using Student-Newman-Keuls multiple range tests.

Colony	1984[1]				1985[2]				1986[3]			
	Date	Mean	S.D.	n	Date	Mean	S.D.	n	Date	Mean	S.D.	n
Lucy	4-7	7.3	4.5	38	13-17	20.4	6.0	30	7-8	20.3	5.4	21
Pine	13-17	11.4	5.0	68	14-15	22.9	6.2	53	12-15	17.7	4.7	59
Tri.	12-14	16.0	5.5	53	11-12	23.7	8.4	49	9	15.2	6.7	40

Colony * Year F = 12.0, df = 4,410, P < 0.0001

[1]	F = 32.6, df = 2,156, P < 0.00001	T > P > L
[2]	F = 2.08, df = 2,129, P = 0.12	L = P = T
[3]	F = 6.2, df = 2,117, P < 0.0028	L > P > T
L	F = 67.1, df = 2,86, P < 0.00001	85 = 86 = 84
P	F = 70.7, df = 2,177, P < 0.00001	85 > 86 > 84
T	F = 21.6, df = 2,139, P < 0.00001	85 > 86 = 84

Table 2: Growth rates (g/day) as measured from composite curves representing a hypothetical nestling on Lucy (L), Pine (P), and Triangle (T) islands in 1984-86. 'n' is the number of chicks from which two measurements were taken. See text for an explanation of the statistics.

Colony	1984[1]			1985[2]			1986[3]		
	Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.	n
Lucy	8.9	0.4	38	10.8	0.5	30	8.0	0.8	21
Pine	6.2	0.3	68	7.2	0.4	53	5.9	0.4	59
Triangle	6.7	0.3	53	7.4	0.3	49	6.4	0.3	40

[1]	F = 15.0,	df = 2,312,	P < 0.00001
[2]	F = 19.5,	df = 2,258,	P < 0.0001
[3]	F = 4.0,	df = 2,236,	P = 0.019
L	F = 6.8,	df = 2,173,	P = 0.001
P	F = 3.2,	df = 2,354,	P = 0.042
T	F = 3.3,	df = 2,279,	P = 0.037

L > P = T
L > P = T
L > P = T
85 > 86 = 84
85 > 86, 86 = 84, 85 = 84
85 > 86, 86 = 84, 85 = 84

increased from 1984 levels, then decreased in 1986 (Table 2). In all colonies growth in 1985 was significantly faster than in 1986 while no difference was detected between growth rates in 1984 and 1986. On Pine and Triangle however, there was no significant difference in chick growth rates between 1984 and 1985.

Composite growth curves for each colony in each year are shown in Figures 2-4. The line of best fit, representing the growth rate of a hypothetical chick over the range of ages, is shown for each figure. The intercepts and R^2 values of the regression lines are given in Appendix 2.

3.3 Nestling diet

3.3.1 Weight of bill loads

Within years, the weight of bill loads exhibited a pattern of variation similar to the results for growth rate. In all years except 1985 the largest loads were delivered on Lucy although they were not significantly larger than loads on Pine and Triangle (Table 3). In all colonies bill loads were lightest in 1984 and tended to be heaviest in 1985 although no data was available from Triangle in that year. Despite significant differences in the mass of adults from separate colonies (Table 4), those differences do not appear to correspond to variation in bill load mass between colonies (i.e. the largest loads were not delivered on Triangle where adults are largest). It is noteworthy that Harris and Hislop (1978) report no correlation

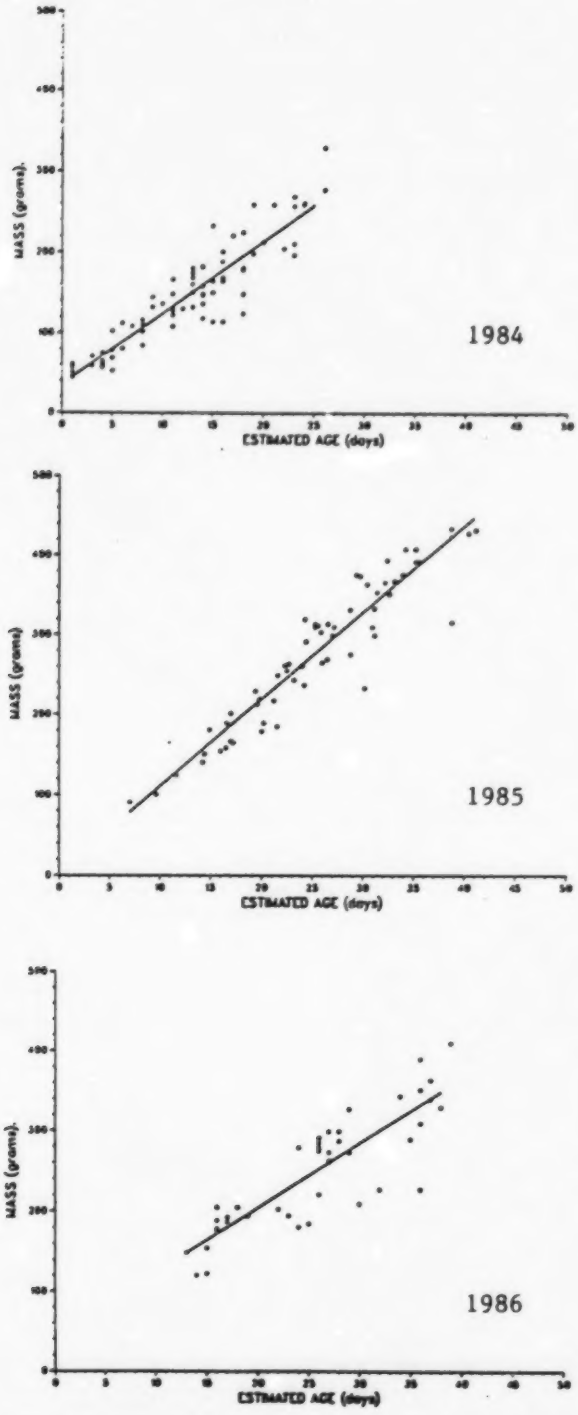

Figure 2: Composite growth curves representing a hypothetical chick fom Lucy Islands in 1984, 1985, and 1986.

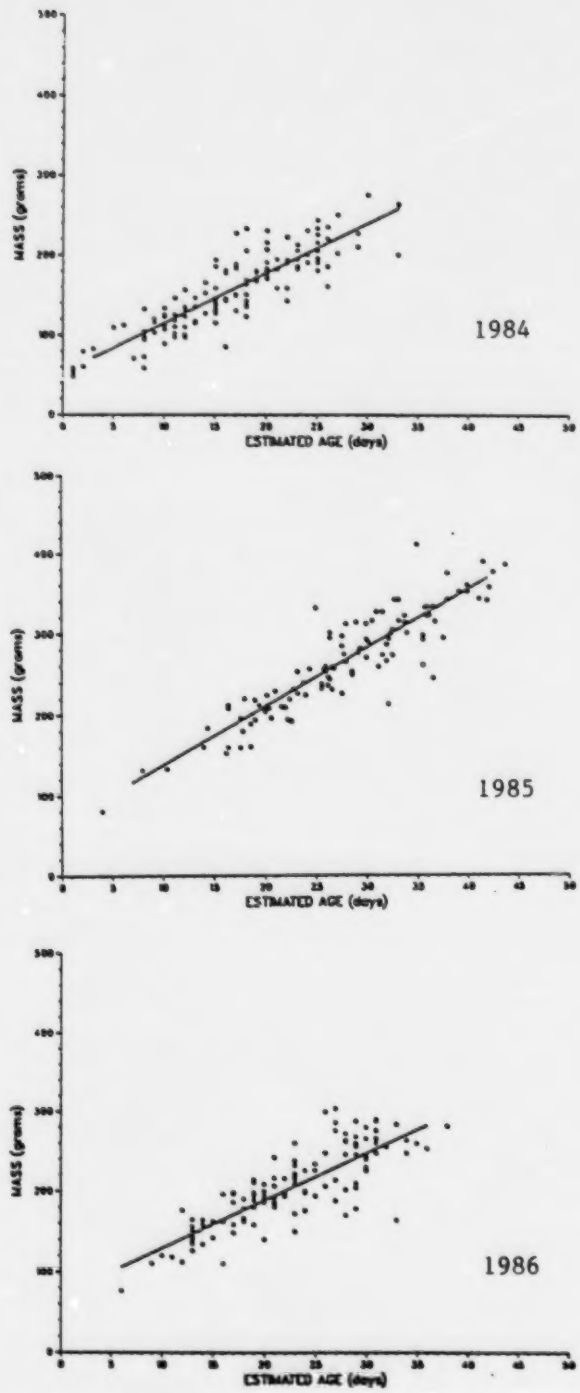

Figure 3: Composite growth curves representing a hypothetical chick fom Pine Island in 1984, 1985, and 1986.

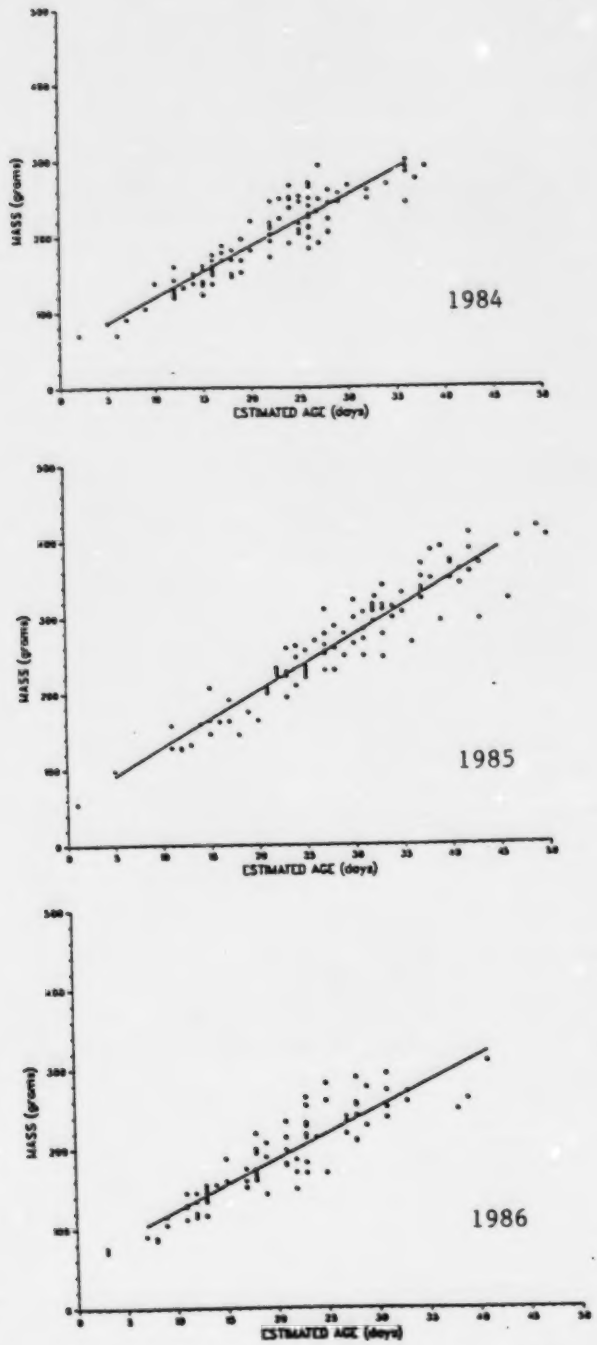

Figure 4: Composite growth curves representing a hypothetical chick fom Triangle Island in 1984, 1985, and 1986.

Table 3: Weights of fish in bill loads (g) taken from adult Rhinoceros Auklets on Lucy (L), Pine (P), and Triangle (T) islands in 1984-86. See Table 1 for a description of the statistics.

Colony	1984[1]			1985[2]			1986[3]		
	Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.	n
Lucy	28.2	8.3	27	33.1	10.5	64	33.9	9.9	61
Pine	23.8	9.9	82	33.9	11.5	55	29.3	12.0	64
Triangle	25.3	9.6	28	-	-	-	31.1	14.0	56

Colony * Year F = 1.54, df = 3,402, P = 0.20

[1]	F = 2.03, df = 2,127,	P = 0.135	L = P = T
[2]	t = 0.39, df = 117,	P > 0.5	L = P
[3]	F = 2.63, df = 2,154,	P = 0.075	L = P = T
L	F = 3.6, df = 2,146,	P = 0.029	85 = 86 > 84
P	F = 13.3, df = 2,191,	P < 0.00001	85 > 86 > 84
T	t = 2.2, df = 82,	P < 0.05	86 > 84

Table 4: Analysis of variance and a Student-Newman-Keuls (SNK) multiple range test of weights of adults from different colonies. The same letter beside two means indicates no significant diference in adult weights based on the SNK test. * = groups significantly different with $\alpha = 0.05$.

Colony	SNK	Mean	S.D.	n	F	P
Lucy	a	514.1	35.9	154		
Pine	a	505.2	38.3	61	4.11	0.017 *
Triangle	b	522.4	30.8	78		

between the weights of adult Atlantic Puffins and their food loads within a single colony.

3.3.2 Composition of bill loads

Table 5 shows the percent composition of sandlance, rockfish and other fish species (combined) in the bill loads collected. A list of other fish delivered to each colony is shown in Appendix 3. On Lucy, sandlance was the dominant prey in all years, representing between 75 and 93 percent of the biomass of bill loads. Although never found on Lucy, rockfish were a common prey on Pine and Triangle in 1984 and 1986. However, in 1985 the quantity of rockfish and other species in bill loads delivered on Pine and Triangle was very low in comparison to the amount of sandlance in bill loads. In 1985, sandlance accounted for over 90 percent of the weight of fish in bill loads on all three colonies.

A t-test comparing bill loads from Pine Island composed only of rockfish with sandlance-only loads showed that bill loads of sandlance were significantly heavier than those with rockfish (Table 6).

3.3.3 Year-classes of sandlance in bill loads

In 1985, the year when sandlance were the dominant prey on all colonies (Table 5), the proportion of year-class-1 fish was larger than in 1984 or 1986 (Table 7). Simultaneously, the proportion of year-class-2 sandlance was lower in 1985 than 1984 or 1986. Following the preponderance of year-class-1 fish in

Table 5: Percent composition (No. = number; B. = biomass in grams) of fish in bill loads taken from Rhinoceros Auklets on Lucy, Pine, and Triangle islands in 1984-86.

Year	Colony	Sandlance		Rockfish		Other		Weight of fish (g)	No. of fish	No. of bill loads
		No.	B.	No.	B.	No.	B.			
1984	Lucy	83	75	0	0	17	25	743	135	27
	Pine	36	20	54	40	10	40	1876	529	82
	Triangle	11	7	80	62	9	31	708	219	28
1985	Lucy	99	93	0	0	1	7	2179	548	64
	Pine	96	92	2	1	2	7	1864	692	55
	Triangle	89	90	10	9	1	1	462	279	13†
1986	Lucy	97	92	0	0	3	8	2100	372	38†
	Pine	34	52	47	19	19	29	1872	451	64
	Triangle	34	48	45	12	21	40	1742	318	56

† Burrow loads

Table 6: Comparison of mean sizes (g) of bill loads composed only of rockfish or only of Pacific sandlance at Pine Island in 1984 and 1986.

Year	Rockfish			Sandlance		
	Mean	S.D.	n	Mean	S.D.	n
1984[1]	20.1	4.3	28	30.4	5.7	7
1986[2]	18.5	4.8	13	39.5	10.6	16

[1] $t = 4.5$, $df = 7.8$, $P = 0.003$
[2] $t = 10.6$, $df = 21.8$, $P < 0.0001$

Table 7: Proportion of year-class-1 and year-class-2 Pacific sandlance in all the bill loads (combined) collected in each year on Lucy, Pine, and Triangle islands in 1984-86.

Year	Colony	Year-class-1		Year-class-2		Mass of fish (g)	No. of fish	No. of bill loads
		No.	Biom.	No.	Biom.			
1984	Lucy	45	25	55	75	874	159	27
	Pine	95	84	5	16	359	164	82
	Triangle	88	48	12	52	134	34	28
1985	Lucy	75	42	25	58	3194	774	64
	Pine	93	86	7	14	1712	619	55
	Triangle	99	97	1	3	437	216	13 †
1986	Lucy	62	39	38	61	2636	509	38 †
	Pine	26	21	74	79	924	134	64
	Triangle	27	22	73	78	837	112	56

† Burrow loads

1985, proportions of year-class-2 fish reached their highest values on Pine and Triangle the following year.

3.3.4 Caloric values of bill loads

The estimated caloric values of bill loads showed a similar pattern of variation to the weights of bill loads (Table 8). In all years except 1985 the loads on Lucy had higher caloric content than bill loads on Pine or Triangle although that difference was only significant in 1984.

The loads with the greatest caloric content tended to be delivered in 1985 while on all colonies caloric values were smallest in 1984.

Table 8: Estimated caloric values (kilocalories) of bill loads taken from Rhinoceros Auklets on Lucy (L), Pine (P) and Triangle (T) islands in 1984-86. See Table 1 for a description of the statistics.

Colony	1984[1]			1985[2]			1986[3]		
	Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.	n
Lucy	152.1	49.8	27	167.1	58.1	64	178.4	33.6	34†
Pine	123.5	51.7	82	167.4	64.5	55	150.4	66.2	64
Triangle	121.4	47.2	28	-	-	-	157.6	74.1	56

† Calculated from burrow loads

Colony * Year F = 1.9, df = 3,404, P = 0.13

[1]	F = 3.4, df = 2,133, P = 0.035	L > P = T
[2]	t = 0.45, df = 113, P > 0.5	L = P
[3]	F = 2.2, df = 2,151, P = 0.117	L = P = T
L	F = 2.2, df = 2,119, P = 0.11	84 = 85 = 86
P	F = 8.9, df = 2,194 P = 0.0002	85 = 86 > 84
T	t = 2.8, df = 2,86 P < 0.01	86 > 84

4. DISCUSSION

The most striking outcome of this study is the consistent ranking of chick growth rates on the three colonies in each year and the fact that growth rates of chicks in all colonies appeared synchronized. We suggest that these results may reflect fluctuations in fish availability, and in particular, sandlance populations.

Inter-year variations in growth reported for Rhinoceros Auklets and Tufted Puffins (Lunda cirrhata) on Triangle Island have been attributed to changes in availability of fish prey, particularly sandlance, between years (Vermeer and Cullen, 1979; Vermeer et al., 1979; Vermeer, 1980). Similarly, researchers working in Washington state attributed differences in growth rates between years on Destruction and Protection islands to changes in feeding conditions (Leschner, 1976; Wilson, 1977). Slow growth of Tufted and Horned Puffins (Fratercula corniculata,) on Buldir Island in Alaska has been associated with poor feeding conditions by Wehle (1983). Among Atlantic Puffins, slow chick growth, retarded fledging and low fledging weights as a result of food shortages have been reported by Nettleship (1972), Harris (1980) and Barrett et al. (1987). This latter study which examines 12 colonies over a three year period is the most convincing since it presents evidence which suggests a direct relationship between the level of herring stocks and breeding success.

In all colonies chick growth rates were significantly faster in 1985 than in 1986 which did not differ from 1984 (Table 2). The mass of sandlance delivered to the colonies exhibited a similar trend (Tables 5, 6). In 1985, sandlance became the dominant prey in all colonies, accounting for over 90% of the biomass of fish delivered to nestlings. In addition, the majority of those fish were first year sandlance, suggesting the presence of a strong year-class-1 in 1985.

Researchers working on Rhinoceros Auklets nesting in Washington state between 1974 and 1983 found that bill loads taken from Protection Island were dominated (% weight) by sandlance and weighed significantly more than loads from Destruction Island where few sandlance were delivered (Wilson and Manuwal, 1986). In addition, they found that chicks on Protection Island consistently grew faster and reached heavier peak and fledging weights than conspecifics on Destruction Island. Similarly, in all years, nestlings on Lucy were fed primarily sandlance and grew significantly faster than chicks on Pine and Triangle Islands (Table 2), which received far less sandlance except in 1985 (Table 5). Although the weights of the bill loads followed the same general pattern within years as the growth rates, none of those differences were significant (Table 3).

An additional explanation for the variation in growth rates between colonies and years may be differences in caloric content of the bill loads. While the differences in caloric content

follow the same pattern as bill load weights, the only significant difference within years was in 1984 when bill loads on Pine and Triangle were composed of rockfish, versus sandlance on Lucy. In addition to the size difference (Table 6) this reflects low caloric value of rockfish in relation to sandlance (Vermeer and Devito, 1986).

Clearly the weight and caloric content of bill loads is insufficient to account for all of the observed variation in growth rates. For example, how can we account for the difference in growth between Lucy and Pine in 1985 when the weight and caloric content of bill loads were indistinguishable? Furthermore, why did chicks on Pine and Triangle not grow more slowly in 1984 when bill loads were significantly lighter and lower in caloric content than in 1986? A factor that may contribute to variation in growth rates, but remains to be studied in detail, is the frequency with which meals are delivered. It has been assumed that Rhinoceros Auklets are fed twice each night (once by each parent, Richardson, 1961; Vermeer and Devito, 1980; Wilson and Manuwal, 1986), however, this may not be the case. While two feeds per night are common, chicks regularly receive only one bill load and sometimes no food on a given night (Bertram, 1988). As a result, differential growth rates of chicks fed loads of similar size and content, on two colonies, may be due to a difference in the average nestling feeding rate during the period in which growth was studied. Feeding rate may also change with the age of the chick (Bertram, 1988). However, this is a variable which cannot be measured when

only bill loads are sampled. The successful use of the hooding technique to obtain food samples from known age birds is described by Hatch (1984) and Bertram (1988).

In nearly all studies of puffins in both the Pacific and Atlantic oceans, sandlance (Ammodytes spp.) were the most important or among the most important prey fed to nestlings (Pearson, 1968; Corkhill, 1973; Harris and Hislop, 1978; Wehle, 1983; Hatch, 1984; Vermeer and Westrheim, 1984; Hislop and Harris, 1983; Wilson and Manuwal, 1986; Furness and Barrett, 1985; Barrett et al., 1987). Why is this so? Foraging theory (see Stephens and Krebs, 1986 for a comprehensive review) states that animals should select prey according to their profitability - the quotient of the amount of energy in a prey item and the amount of time taken to capture and handle the prey. Animals should selectively choose the most profitable (or optimal) prey when abundance is high. An explicit prediction of optimal diet theory is that lower ranked prey, regardless of their abundance, should be taken only when higher ranked prey are scarce.

That Atlantic Puffins fish selectively was demonstrated by Harris and Hislop (1978) working in Scotland. They showed that sprats (Sprattus sprattus) dominated bill loads even though they were outnumbered by other prey found in trawl catches made in puffin feeding areas. On St. Kilda, in 1975 and 1976, when sprats were the most important food the weights of recently fledged young were significantly higher than in 1973 and 1974 when whiting (Merlangius merlangius) made up over 50% of the

biomass fed to the young. Harris and Hislop (1978) note that young puffins can be easily reared in captivity on a diet of sprats but perish when fed only whiting. They suggested that whiting were taken only when other food was scarce.

We propose that variations in growth rates of Rhinoceros Auklets nesting in B.C. may result from similar fluctuations in prey abundance and availability thus leading to 'good' and 'bad' years for growth as observed on St. Kilda. The fact that growth rates on all colonies were highest in 1985 when sandlance predominated bill loads suggests that sandlance were abundant along the northern B.C. coast that year and furthermore, that sandlance are a preferred prey for Rhinoceros Auklets. The lower growth rates on all colonies in 1984 and 1986 suggests that sandlance abundance was low, especially in 1984 when rockfish were the dominant prey on Pine and Triangle islands. Further evidence that 1984 was a poor year for sandlance, and hence chick growth, comes from a second composite growth study, conducted on Triangle Island that year. During the second period, sandlance virtually disappeared from the nestling diet. Chicks of the same weight at the beginning of the two growth phases grew significantly slower in the second ten day interval. Moreover, nine chicks (17%) were starving and lost weight during the period, something which never occurred in the first period (Bertram, unpublished).

In comparison to 1985 and 1986, chicks excavated on Pine and Triangle in 1984 were relatively young (Table 1), suggesting

that breeding was delayed, possibly as a result of a food shortage.

The most convincing study to date that shows a close correspondence between seabird breeding success and ocean feeding conditions was conducted in Norway from 1980 to 1983 by Barrett et al. (1987). Between 1980 and 1982 breeding success of Atlantic Puffins on 6 colonies off the north coast of Norway ranged from "poor" to "total failure". However, in 1983 breeding success on all colonies improved markedly, presumably due to the increase in quality and quantity of food. In 1983, the first year since the collapse of the Norwegian spring spawning stock in the late 1960's and early 1970's, the O-group stock was large, reaching a level of about 30 times the average strength of year-classes 1975-82 (Barrett et al., 1987).

Another study on Atlantic Puffins attempts to relate changes in the food of nestlings to independent estimates of fish stocks (Hislop and Harris, 1983). They report a progressive replacement of sprats by herring in the food loads delivered to nestlings on the Isle of May between 1978 and 1982. They attribute the changes in the numbers of those fish to the decline in the North Sea sprat population and the increase in the number of young herring that occurred between 1980 and 1982. It is noteworthy that while herring stocks in 1973 and 1974 were of comparable size to the 1980's levels, no herring were found in the food loads delivered to young in those years. Hislop and Harris (1983) attribute that phenomenon to local changes in herring

availability that may occur "irrespective of changes in the total population numbers". While this may be true it is difficult to address without comparable data from other colonies in Scotland. An alternative explanation is that herring were not selected by puffins in 1973 or 1974 because more profitable sprats were present in large numbers.

In summary, the results of this study indicate that sandlance availability is related to inter-year and inter-colony variation in the rate of chick growth in Rhinoceros Auklets breeding in B.C. That chick growth is most rapid when sandlance is the principal prey in the diet suggests that these fish are the preferred prey for this seabird. The large numbers of year-class-1 sandlance relative to year-class-2 fish on all colonies in 1985 suggests that sandlance abundance covaries across broad geographic areas. As such, the composite curves of Rhinoceros Auklet chick growth, combined with information on nestling diet, may be used to make inferences about abundance of these fish in July, when they are commonly the dominant prey in B.C. (Vermeer and Westrheim, 1984). However, such inferences should not be made if data are collected from only one colony. In such a case, changes in chick growth rates or diet may not reflect varying fish abundance but rather a change in the distance of fish schools from a colony, which may result in parents altering bill load size or provisioning rate. Alternatively, adults may adjust their foraging effort in order to compensate for variations in prey abundance such that nestling growth rates may remain unaltered over time while fish

abundance changes. At present few details are known about variation in parental provisioning effort in relation to feeding conditions, and until such information is available composite chick growth data from a single seabird colony may be limited in scope. As Vermeer and Westrheim (1984) point out, complimentary ocean sampling with nets is necessary to establish the actual relationships of juvenile fishes in marine waters to those observed in the diet of nestling Rhinoceros Auklets. That procedure, however, is very costly. Similar concurrent changes in nestling diet and composite chick growth on well separated colonies allows researchers to make inferences about the abundance of prey species from year to year. Therefore, monitoring seabird growth and diet could be an affordable source of information for wildlife managers on the stresses facing seabird populations.

5. MANAGEMENT RECOMMENDATIONS

In combination with Vermeers' early work on the Rhinoceros Auklet in B.C. (1979, 1980; Vermeer and Cullen, 1979, 1982; Vermeer and Westrheim, 1984), this study provides further baseline information for a long-term monitoring program for this species in B.C. In Britain and Norway intensive studies of breeding populations of Atlantic Puffins for over 20 years have been invaluable in detecting changes in the size of breeding populations as well as trends in abundance of prey populations of fish. In B.C. the need for a seabird monitoring plan has intensified as a result of two factors. The first is the threat to seabird populations from pending offshore oil exploration and development in coastal waters. The second factor is the possible increased importance of sandlance as an alternative prey to herring, which, in B.C., presently exceeds any single commercial fish in landed value (Taylor, 1985). The rise and subsequent collapse of three major herring fisheries - the southern North Sea stock, the Hokkaido-Sakhalin stock, and the Arcto-Norwegian stock (Ware, 1985) was emulated by the B.C. herring stocks which collapsed in the late 1960s (Taylor, 1985). Although the stocks 'recovered' in the early 1970s, the combination of the high market value and the difficulties in managing the fishery (Taylor, 1985) make the future of B.C. herring stocks tenous. Many marine animals in B.C., including commercially important species such as Chinook and Coho salmon (Oncorhynchus tshawytscha and Oncorhynchus kisutch respectively), feed

extensively on both herring and sandlance (Hart, 1980). In the event of a decline in herring stocks, such predators may resort to sandlance as their pricipal prey. As a result, sandlance populations could decline with seabird numbers following suit. In Britain, food shortage was cited as one of the main causes for the decline of Atlantic Puffins breeding on St. Kilda in the Outer Hebrides (Harris, 1978). Recent news items quoting Harris (anon. 1988a,b) attribute the 1988 breeding failure of Atlantic Puffins on the Isle of May directly to the disappearance of sandlance.

We suggest that the Rhinoceros Auklet represents an ideal indicator species for a long-term monitoring program in B.C. for the following reasons: 1) Rhinoceros Auklets are located on several well separated, large, easily accessible colonies; 2) adults feed young whole fish carried cross-wise in the bill, thus making food sampling relatively easy and effective; 3) adults only visit the young at night thus making it possible for workers to handle young without interrupting parent-offspring interactions; 4) food can be obtained from chicks of known age using the hooding technique; and 5) there exists an established baseline data set for three of the largest colonies on the coast.

Monitoring could entail the construction of composite growth curves and sampling of both bill loads and burrow loads (using the hooding technique on known age birds) on a few colonies, visited synchronously. The regularity of visits will depend on

the desired level of sensitivity of the monitoring program. The most sensitive assay would involve visits every year, while visits every fifth year will lead to slower detection of any developing trends in feeding conditions. This method offers the practical advantage that a small team (four) could conduct the project at two separate sites using only two, three to four day visits at each site, 10 days apart. The method is also applicable to Cassin's Auklet (Ptychoramphus aleuticus) and Tufted Puffins although food studies may present problems. Cassin's Auklets feed their young on a plankton slurry carried in a gular pouch. That makes quantitative food sampling and identification difficult. The Tufted Puffin feeds its young throughout the day, a fact that may preclude them from this approach to monitoring since parent-offspring interactions are likely to be severely disturbed (Hatch,1984).

The most logical choices for study sites are Lucy and Pine islands. In addition to their similar low-lying topography and inshore locations, they are among the most accessible colonies in B.C. To facilitate efficient monitoring by eliminating time-consuming and destructive excavation, artificial burrows could be placed in each colony (similar to those proven successful on Protection Island in Washington (Wilson, 1986). Thirty six artificial burrows were implanted on Lucy Island in April 1987. Twenty nine percent showed signs of visitation when examined in August of that year suggesting that they will be adopted. The existence of artificial burrows may also facilitate a more detailed investigation of parent-offspring interactions,

information which will be important in developing a monitoring program (see below). By fitting the artificial burrow with an electronic scale to weigh adults as they enter and exit (with and without fish), complete 'burrow histories' can be obtained (this type of scale is presently under development at Simon Fraser University). Such data will help elucidate details of the nature of parental investments in these birds.

While it is generally accepted that seabirds can act as indicators of marine ecological processes, the extent to which this is true is presently limited in scope owing to the scarcity of answers to some fundamental questions pertaining to the life histories fo seabirds. How parental effort changes in relation to the age of young and ocean feeding conditions is a complex problem that has received little attention (but see Bertram, 1988). How hard are parents willing to work when raising young and how could this affect the detection of trends in the abundance of prey populations are other important unanswered questions. The elucidation of these types of problems in parental investment will lead to the development of new, or refinement of existing models that will allow us to predict patterns of breeding behavior (e.g. provisioning) in response to changes in ocean feeding conditions or perturbations to the environment caused by events such as oil spills (e.g. Ford et al., 1982).

Research in Behavioural Ecology that helps to unravel questions about parental investment in the Rhinoceros Auklet

will not only lead to a greater understanding of seabird life histories in general, but will also fuel the development of a monitoring program that enhances the ability of wildlife managers to use information collected on Rhinoceros Auklet colonies to make inferences about marine resources. Clearly, more information about the dynamics of fish prey populations would accelerate the progress of seabird research in B.C. and increased collaboration between the Canadian Wildlife Service and the Department of Fisheries and Oceans would be beneficial.

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APPENDIX 1: THE PILOT STUDY ON LUCY ISLANDS IN 1983

In 1983 researchers visited Lucy Islands to assess the feasibility of using Rhinoceros Auklets for conducting a study of growth (using the composite technique of Ricklefs and White, 1975) and diet. All of the methods are identical to those described in section 2. The following is an outline of the results of that work.

Chick age at first weighing

The first measurements of chicks occurred between 13 - 17 July. During that period chicks were, on average 20.9 days old (S.D. = 7.0, n = 42).

Chick Growth

Ages of chicks in the composite growth study ranged from 4 to 45 days old. The slope of the growth curve (g/day) was 7.2. The intercept and R^2 value of the regression line is included in Appendix 2.

Nestling Diet

Bill loads weighed, on average 30.7 g (S.D. = 8.6, n = 42). Loads consisted primarily of Pacific sandlance (% number = 97, % biomass = 91, the remainder were not identified) In total 290 fish weighing a combined 1269 g were collected. Among the sandlance, year-class-1 fish constituted a greater proportion of the nestling diet (% number = 85, % biomass = 75) than year-class-2 (% number = 15, % biomass = 25).

APPENDIX 2. EQUATIONS OF COMPOSITE GROWTH CURVES

Table App.2.1: Coefficients for linear regression equations fitted to the composite growth curves from Lucy, Pine and Triangle Islands in 1983 - 86. 'a' = the y intercept and 'b' = the slope.

Year	Colony	a	b	R^2	n
1983	Lucy	66.0	7.2	0.83	42
1984	Lucy	35.1	8.9	0.85	38
	Pine	52.3	6.3	0.78	68
	Triangle	51.2	6.7	0.84	53
1985	Lucy	2.3	10.8	0.88	30
	Pine	66.0	7.2	0.75	53
	Triangle	53.2	7.4	0.89	49
1986	Lucy	44.4	8.0	0.72	21
	Pine	69.7	5.9	0.65	59
	Triangle	58.5	6.4	0.82	40

APPENDIX 3: ADDITIONAL PREY SPECIES OF RHINOCEROS AUKLETS

Table App.3.1: Prey species (other than Pacific sandlance or rockfish) in bill loads collected on Lucy, Pine and Triangle Islands in 1984-86. Prey are catagorized according to the scheme used by Vermeer and Westrheim (1984). Species are denoted as principal (P) if they constituted more than 10% of the biomass (g) of the combined bill load weight and labelled as common (C) if they fell below that level. Prey species that occurred not more than six times in the study are referred to as occasional (O).

Year	Prey Species	Lucy	Pine	Triangle
1984	Kelp greenling[3]	-	-	O
	Pacific herring[4]	P	P	-
	Pacific saury[6]	-	C	P
	Salmon[9]	P	P	-
	Sablefish[8]	-	-	O
1985	Kelp greenling	O	C	O
	Lingcod[2]	O	-	-
	Pacific herring	C	C	-
	Pacific sandfish[5]	O	-	-
	Salmon	C	C	-
	Surf Smelt[10]	O	-	-
	Squid[11]	-	O	-
1986	Bluethroat argentine[1]	-	C	-
	Kelp greenling	-	O	C
	Pacific herring	C	C	-
	Pacific saury	-	C	P
	River lamprey[7]†	O	-	-
	Sablefish	-	O	C
	Salmon	C	P	-
	Squid	-	O	O
	Tube-snout[12]†	O	-	-

[1]Nansenia candida [2]Hexagrammos decagrammus [3]Ophiodon elongatus
[4]Clupea harengus [5]Trichodon trichodon [6]Cololabis saira
[7]Lampetra ayresi [8]Anoplopoma fimbria [9]Onchorynchus spp.
[10]Hypomesus pretiosus [11]Unidentified [12]Aulorhynchus flavidus
† Never before reported in diet (sampled on 6 August)